The Tortoise and the Hare: Interactions between Reinforcement Learning and Working Memory

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Abstract

■ Learning to make rewarding choices in response to stimuli depends on a slow but steady process, reinforcement learning, and a fast and flexible, but capacity-limited process, working memory. Using both systems in parallel, with their contributions weighted based on performance, should allow us to leverage the best of each system: rapid early learning, supplemented by long-term robust acquisition. However, this assumes that using one process does not interfere with the other. We use computational modeling to investigate the interactions between the two processes in a behavioral experiment and show that working memory interferes with reinforcement learning. Previous research showed that neural representations of reward prediction errors, a key marker of reinforcement learning, were blunted when working memory was used for learning. We thus predicted that arbitrating in favor of working memory to learn faster in simple problems would weaken the reinforcement learning process. We tested this by measuring performance in a delayed testing phase where the use of working memory was impossible, and thus participant choices depended on reinforcement learning. Counter-intuitively, but confirming our predictions, we observed that associations learned most easily were retained worse than associations learned slower: Using working memory to learn quickly came at the cost of long-term retention. Computational modeling confirmed that this could only be accounted for by working memory interference in reinforcement learning computations. These results further our understanding of how multiple systems contribute in parallel to human learning and may have important applications for education and computational psychiatry. ■

INTRODUCTION

When facing a challenge (such as responding to a natural disaster), we often need to pursue two solutions in parallel: emergency measures for the immediate future and carefully thought-out long-term plans. These measures make different trade-offs between speed and efficiency, and neither is better than the other in absolute. Allocating finite resources to multiple strategies that involve such different trade-offs can mitigate their limitations and make use of their benefits. Recent work shows that human learning, even in very simple environments, follows this principle: It involves multiple parallel neurocognitive systems that arbitrate differently between immediate, effortful efficacy and slower, long-term robustness (Bornstein, Khaw, Shohamy, & Daw, 2017; Collins & Frank, 2012; Daw, Gershman, Seymour, Dayan, & Dolan, 2011; Poldrack et al., 2001). In this article, we present a new experiment to computationally characterize how these systems work together to accomplish short- and long-term learning.

We focus on two well-defined systems: reinforcement learning (RL) and working memory (WM). WM enables fast and accurate single-trial learning of any kind of information, with two limitations—a capacity or resource limit and a temporal limit, such that we can only accurately remember a small amount of information for a short time, after which we may forget (Baddeley, 2012). RL, in contrast, enables slower but robust reward-based learning of the value of choices (Dayan & Daw, 2008). Separable (yet partially overlapping) brain networks support these two systems: WM is centrally dependent on pFC (Cools, 2011; Miller & Cohen, 2001), whereas RL relies on dopaminergic signaling in the striatum (Schultz, 2013; Tai, Lee, Benavidez, Bonci, & Wilbrecht, 2012; Frank & O'Reilly, 2006; Montague, Dayan, & Sejnowski, 1996). We previously developed a simple experimental protocol to show that both systems are used in parallel for instrumental learning (Collins, Ciullo, Frank, & Badre, 2017; Collins & Frank, 2012). In this protocol, participants used deterministic feedback to learn the correct action to pick in response to a stimulus; critically, in different blocks, they needed to learn associations for a different number of stimuli in a new set. This set size manipulation allowed us to disentangle the contributions of WM to learning from those of RL, because WM is capacity limited (Cowan, 2010), whereas RL is not. In particular, this manipulation was essential in identifying which of the systems was causing learning dysfunction in clinical populations (Collins, Albrecht, Waltz, Gold, & Frank, 2017; Collins, Brown, Gold, Waltz, & Frank, 2014).

However, how the two systems interact is still poorly understood. Previous models assumed that the RL and WM systems compete for choice but otherwise learn

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independently of each other. In particular, if RL was fully independent from WM, values learned through RL should only depend on reward history and be independent of set size. Recent evidence shows that this may not be the case and that WM may instead interfere in RL computations. Indeed, in an fMRI study, we showed that RL signals were blunted in low set sizes, when WM was sufficient to learn stimulus–response associations (Collins, Ciullo, et al., 2017). These results were confirmed in an EEG study (Collins & Frank, in press), where we additionally found that trial-by-trial markers of WM use predicted weaker RL learning signals. Last, we found behavioral evidence that the value of different items was better retained when learned under high load than under low load (Collins, Albrecht, et al., 2017), again hinting at an interference of WM with RL computations. Together, these results hint at a mechanism by which RL learning is weakened in low set sizes, when WM is most successful. We hypothesize that successful WM use (in particular, in low set sizes) may interfere with RL, either by inhibiting learning or, more consistently with our most recent EEG findings, by communicating to the RL system its quickly acquired expectations and thus making positive reward prediction error (RPE) signals less strong.

In this project, we further investigate the nature of interactions between WM and RL during learning. Specifically, we propose an improvement to our previous protocol that allows us to (1) characterize short-term learning versus long-term learning and retention, (2) investigate how WM use impacts both forms of learning, and (3) computationally characterize the complete, integrated, interactive learning process. In the new protocol (Figure 1A), the learning phase includes multiple blocks of one of two set sizes—low (3) and high (6); after a short irrelevant task to provide a delay, the experimental protocol ends with a surprise testing phase in extinction to assess the retention of the associations acquired during the learning phase. This testing phase probes how well participants remember the correct choice for all the stimuli they learned previously. We hypothesize that WM plays no direct role in testing phase choices (Figure 1B) because, in the absence of feedback, no new information is available in the testing phase: Participants decide based on experience acquired more than 10 min prior, for 54 different stimulus–action associations, both beyond the extent of WM maintenance. Thus, the testing phase serves as a purer marker of RL function than could be obtained with the original design (Collins & Frank, 2012), allowing us to observe how RL-learned associations depend on the learning context (high/low set size) and thus to investigate the interaction of WM and RL.

On the basis of our previous imaging results showing blunted RL signals in low set sizes, we made the

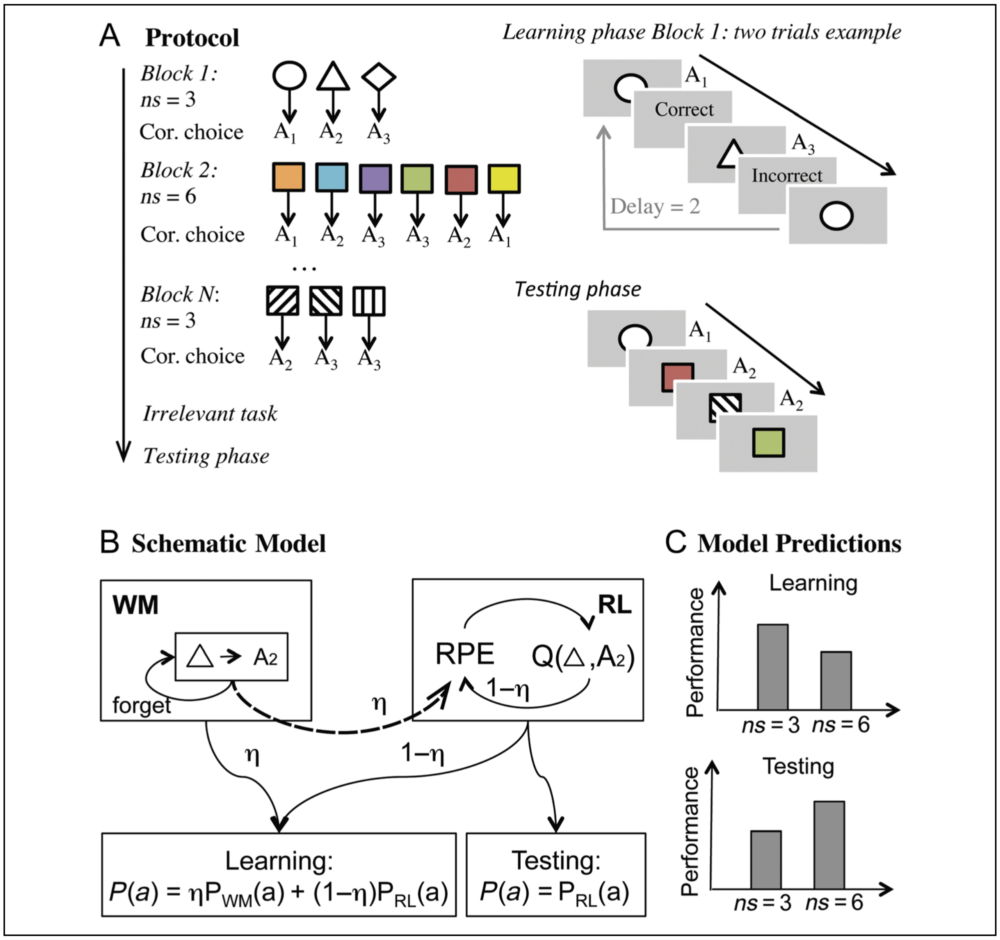


Figure 1. (A) Experimental protocol. (Left) The experiment includes a learning phase with 14 learning blocks of set size $ns = 3$ or 6, followed by a short irrelevant task and a surprise testing phase. (Right) Examples of learning phase and testing phase trials. (B) Schematic model. We assume that WM and RL both contribute competitively to choice during learning; the weight η of WM versus RL for choice depends on the capacity and set size. WM stores exact information but may forget; RL learns from RPEs the value of selecting an action for a given stimulus (e.g., the triangle). We additionally hypothesize that WM influences RL computations (dashed arrow) by contributing expectations to the computation of the RPE. Testing phase does not involve WM contributions, but only RL. (C) Model predictions (schematic): If $\eta(ns = 3) < \eta(ns = 6)$, the model predicts worse performance under high load during learning; however, items learned under high load are predicted to be better retained during testing, because WM interferes less with RL.

counterintuitive prediction that retention of associations learned under low set sizes would be worse than that in high set sizes (Figure 1C). Furthermore, we predicted that a model incorporating interference of WM in RL computations (Figure 1B; Methods) would capture behavior better than models assuming either single systems or independent WM and RL modules competing for choice.

METHODS

Participants

We first tested 49 University of California, Berkeley (UCB), undergraduate students (31 women; aged 18–40 years, mean = 20.5 years). To replicate the results obtained with this first sample, we then tested a second independent sample, which included 42 UCB undergraduate students (26 women; aged 18–29 years, mean = 20.7 years). Because the effects in the second sample fully replicated the results obtained with the first sample, we report here the results with participants pooled together. We excluded six participants based on poor overall performance in the task indicating lack of involvement (less than 75% average accuracy at asymptotic performance). The final sample included n = 85 participants. All participants provided written informed consent, and the Committee for the Protection of Human Subjects at UCB approved the research.

Experimental Protocol

General

The methods are modified from previous published versions of this experimental protocol (Collins & Frank, 2012, in press; Collins, Albrecht, et al., 2017; Collins, Ciullo, et al., 2017; Collins et al., 2014). Participants performed a learning experiment in which they used reinforcement feedback ("+1" or "0") to figure out the correct key to press in response to several visual stimuli (Figure 1A). The experiment was separated into three phases: a learning phase comprising multiple independent learning blocks (mean duration = 26 min, range = 22–34 min), an unrelated memory task (mean duration = 11 min, range = 10–16 min), and a surprise testing phase assessing what was retained from the learning phase (mean duration = 7 min, range = 6–8 min).

Learning Phase

The learning phase was separated into 14 blocks, with a new set of visual stimuli of set size ns in each block, with $ns = 3$ or ns = 6. Each block included 12–14 presentations of each visual stimuli in a pseudorandomly interleaved manner (controlling for a uniform distribution of delay between two successive presentations of the same stimulus within [1:2 * ns] trials and the number of presentations of each stimulus), for a total of ns * 13 trials. At each trial, a stimulus was presented centrally on a black background. Participants had up to 1.5 sec to answer by pressing one of three keys with their right hand. Keypress was followed by visual feedback presentation for 0.5 sec, followed by a fixation of 0.5 sec before the onset of the next trial. For each image, the correct keypress was the same for the entire block. Pressing this key led to a truthful "+1" feedback, whereas pressing any other key led to a truthful "0" feedback. Failure to answer within 1.5 sec was indicated by a "no valid answer" message. Stimuli in a given block were all from a single category (e.g., colors, fruits, animals) and did not repeat across blocks.

We varied the set size ns across blocks: Of 14 blocks, eight had a set size ns = 3; and six, a set size ns = 6. The first and last blocks of the learning phase were of set size ns = 3. We have shown in previous research that varying set size provides a way to investigate the contributions of capacity- and resource-limited WM to RL.

n-Back

After the learning phase, participants performed a classic visual n-back task (n = 2–5). The purpose of this phase was to provide a time buffer between the learning phase and the surprise testing phase. We do not analyze the n-back performance here.

Testing Phase

At the end of the n-back task, participants were informed that they would be tested on what they had learned during the first phase of the experiment. The testing phase included a single block where all stimuli from the learning phase (excepting Block 1 and Block n to limit recency and primacy effects—thus a total of 54 stimuli: 36 learned in set size 6 and 18 learned in set size 3 blocks) were presented four times each, for a total of 216 trials. The order was pseudorandomized to ensure that each stimulus was presented once in each quarter of the test phase. Each trial was identical to the learning phase, except that no feedback was presented so that participants could not learn during this phase.

Model-Free Analysis

Learning Phase

Learning curves were constructed by computing the proportion of correct answers to all stimuli of each set size as a function of their iteration number. Trials with missing answers were excluded. RT learning curves were limited to correct choices. Asymptotic performance/RTs were assessed over the last six presentations of each stimulus.

We also used a multiple logistic/linear regression analysis to predict correct choices/RTs in the learning phase. The main predictor was the "reward" predictor (#R), which indicated the number of previous correct choices for a given stimulus and was expected to capture the effect of reward history on learning (Collins & Frank, 2012). Predictors expected to capture WM contributions were (1) the set size *ns* of the block in which a stimulus was learned and (2) the delay or number of trials since the participant last selected the correct action for the current stimulus (Figure 1A). Last, we also included the block number to investigate whether exposure to the learning phase modified performance. All regressors were *z* scored before entering into the regression model. For visualization purposes in Figures 2 and 5, weights are sigmoid transformed and scaled to [−1,1] (keeping 0 as the no effect value). Specifically, the transformation is $\beta \leftarrow (2/(1 + \exp(-\beta))) - 1$.

Testing Phase

We computed the performance as the proportion of correct choices separately for stimuli that had been learned in blocks of set size $ns = 3$ or $ns = 6$. We also used multiple logistic/linear regression analysis for the testing phase, with reward, set size, and block regressors. The reward regressor was the asymptotic performance for a given stimulus, and the set size and block regressors were defined as the set size and block number of the block during which a given stimulus had been learned in the learning phase.

Errors

To investigate the types of errors made during the testing phase, we identified a set of stimuli that met the following criteria: (1) the participant had made at least one mistake for that stimulus during the learning phase and (2) one of the two incorrect actions had been selected more often than the other during the learning phase. This allowed us to define for the testing phase a perseverative error as choosing the action that had been selected most and an optimal error as choosing the erroneous action that had been selected least (this would correspond to best avoidance of previously unrewarding actions). We computed the proportion of perseverative versus optimal errors separately for each set size.

Computational Modeling

We simultaneously modeled the learning and testing phases based on our theory, as shown in Figure 1C. The models assume that dynamically changing learned associations control learning phase policy and that policies acquired at the end of the learning phase are used during the testing phase.

Models

We tested three families of models:

- RLs: pure RL models
- RLWM: mixture models with independent WM and RL, where both WM and RL contributed to learning but only RL contributed to testing
- RLWMi: RLWM mixture models with interacting WM and RL, where both WM and RL contributed to learning but only RL contributed to testing

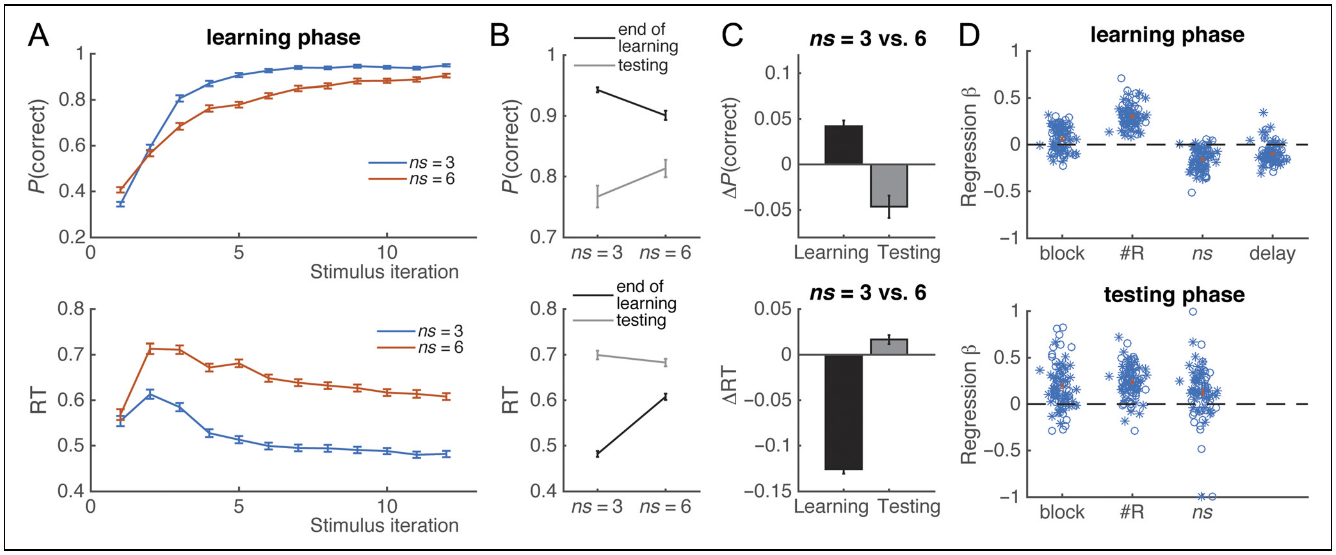


Figure 2. Behavioral results show opposite effect of load in learning and retention. (A, top) Proportion of correct trials as a function of stimulus iteration number, for set sizes *ns* = 3/6. (A, bottom) Same for RTs. (B, top) Proportion of correct trials at asymptotic learning performance (last five iterations of a stimulus: black line) and during test phase (gray line). (B, bottom) RTs for testing and asymptotic learning. (C) Difference between low and high set sizes shows significant, opposite results for the learning and test phases, in both performance (top) and RTs (bottom). (D, top) Transformed logistic regression weights from the learning phase show expected effects of learning block and reward history (due to practice and RL) as well as expected negative effects of set size and delay, characterizing WM contributions. (D, bottom) Transformed logistic regression weights from the test phase also show expected effects of learning block and reward history but show better test phase performance with a higher set size, contrary to the learning phase. Open circles represent individual participants from the original experiment; stars represent individual participants from the replication sample. The results are identical. Error bars indicate *SEM*.

RL models. Computational models in the class of RL models are built off a classic formulation of RL models (see below), with two key parameters—learning rate α and softmax temperature β. We also investigate RL models that include various combinations of additional mechanisms that may help provide a better account of behavior, while remaining in the family of single-process RL models. These additional mechanisms include undirected noise, forgetting, perseveration, initial bias, and dependence of learning rate on task conditions. We describe all mechanisms below.

Classic RL. For each stimulus s and action a, the expected reward $Q(s,a)$ is learned as a function of reinforcement history. Specifically, the Q value for the selected action given the stimulus is updated upon observing each trial's reward outcome r_t (1 for correct, 0 for incorrect) as a function of the prediction error between expected and observed reward at trial t:

$$Q_{t+1}(s,a) = Q_t(s,a) + \alpha \times \delta_t$$

where $\delta_t = r_t - Q_t(s,a)$ is the prediction error and α is the learning rate. Choices are generated probabilistically with greater likelihood of selecting actions that have higher Q values, using the softmax choice policy, which defines the probabilistic rule for choosing actions in response to a stimulus:

$$p(a|s) = \exp(\beta Q(s,a))/\sum_i(\exp(\beta Q(s,a_i)))$$

Here, β is an inverse temperature determining the degree with which differences in Q values are translated into a more deterministic choice, and the sum is over the three possible actions a_i. Choice policy during the testing phase is identical to the policy at the end of the learning phase.

Undirected noise. The softmax allows for stochasticity in choice, but stochasticity is more impactful when the value of each action is close to the values of the alternative actions. We also allow for "slips" of action (i.e., even when Q value differences are large; also called "irreducible noise" or lapse rate). Given a model's policy $\pi = p(a|s)$, adding undirected noise consists in defining the new mixture choice policy:

$$\pi' = (1 - \varepsilon)\pi + \varepsilon U$$

where U is the uniform random policy ($U(a) = 1/n_\mathrm{A}$, with number of actions $n_\mathrm{A} = 3$) and the parameter $0 < \varepsilon < 1$ controls the amount of noise (Collins & Frank, 2013; Collins & Koechlin, 2012; Guitart-Masip et al., 2012). Intuitively, this undirected noise captures a choice policy where, with probability $1 - \varepsilon$, the agent picks choices normally but, with probability ε, the agent lapses and acts randomly. Nassar and Frank (2016) showed that failing to take this irreducible noise into account can make model fits be unduly influenced by rare odd data points (e.g., which might arise from attentional lapses) and that this problem is remedied by using the hybrid softmax-ε-greedy choice function as used here.

Forgetting. We allow for potential decay or forgetting in Q values on each trial, additionally updating all Q values at each trial, according to:

$$Q_{t+1} \leftarrow Q_\mathrm{t} + \phi(Q_0 - Q_t)$$

where $0 < \phi < 1$ is a decay parameter, which at each trial, pulls the estimates of values toward the initial value $Q_0 = 1/n_\mathrm{A}$. This parameter allows us to capture forgetting during learning.

Perseveration. To allow for potential neglect of negative, as opposed to positive, feedback, we estimate a perseveration parameter *pers* such that, for negative prediction errors ($\delta < 0$), the learning rate α is reduced by $\alpha = (1 - pers)\alpha$. Thus, values of *pers* near 1 indicate perseveration with complete neglect of negative feedback, whereas values near 0 indicate equal learning from negative and positive feedback.

Initial bias. Although we initialize the Q values to a fixed value for all stimuli and actions, participants may come in with a preference for pressing Action 1 with their index finger, for example (or other biases). To account for subjective biases in action choices and allow for better estimation of other parameters, we use the first choice made by a participant for each stimulus as a potential marker of this bias and introduce an initial bias parameter *init* that boosts the initial value of this first, before the first learning update. Specifically, the initial bias update is $Q_0(s,a_\mathrm{first}(s)) = 1/n_\mathrm{A} + init * (1 - 1/n_\mathrm{A})$.

Additional mechanisms. We test two additional mechanisms to attempt to provide better fit within the "RL-only" family of models. The first mechanism assumes that learning rates may be different for each set size. The second mechanism assumes that two sets of RL values are learned in parallel and independently, with independent learning rates: One process controls learning phase policy; the other controls testing phase policy only. The best-fitting model in the "RL-only" family of models includes all mechanisms described above, for a total of nine parameters (softmax β, four learning rates [$\alpha_\mathrm{learn}(3)$, $\alpha_\mathrm{learn}(6)$, $\alpha_\mathrm{test}(3)$, $\alpha_\mathrm{test}(6)$], decay, *pers*, undirected noise ε, initial bias). This best model (RLs), in addition to the simplest RL model (for baseline), is simulated in Figure 3 for predictions. The RL model predicts no effect of phase or set size on performance (top row of Figure 3: The two model learning curves are overlapping); the RLs model's predictions are dependent on the values of the four learning rate parameters, but the model is flexible enough to capture opposite effects of set size in the learning and test phases (second row of Figure 3).

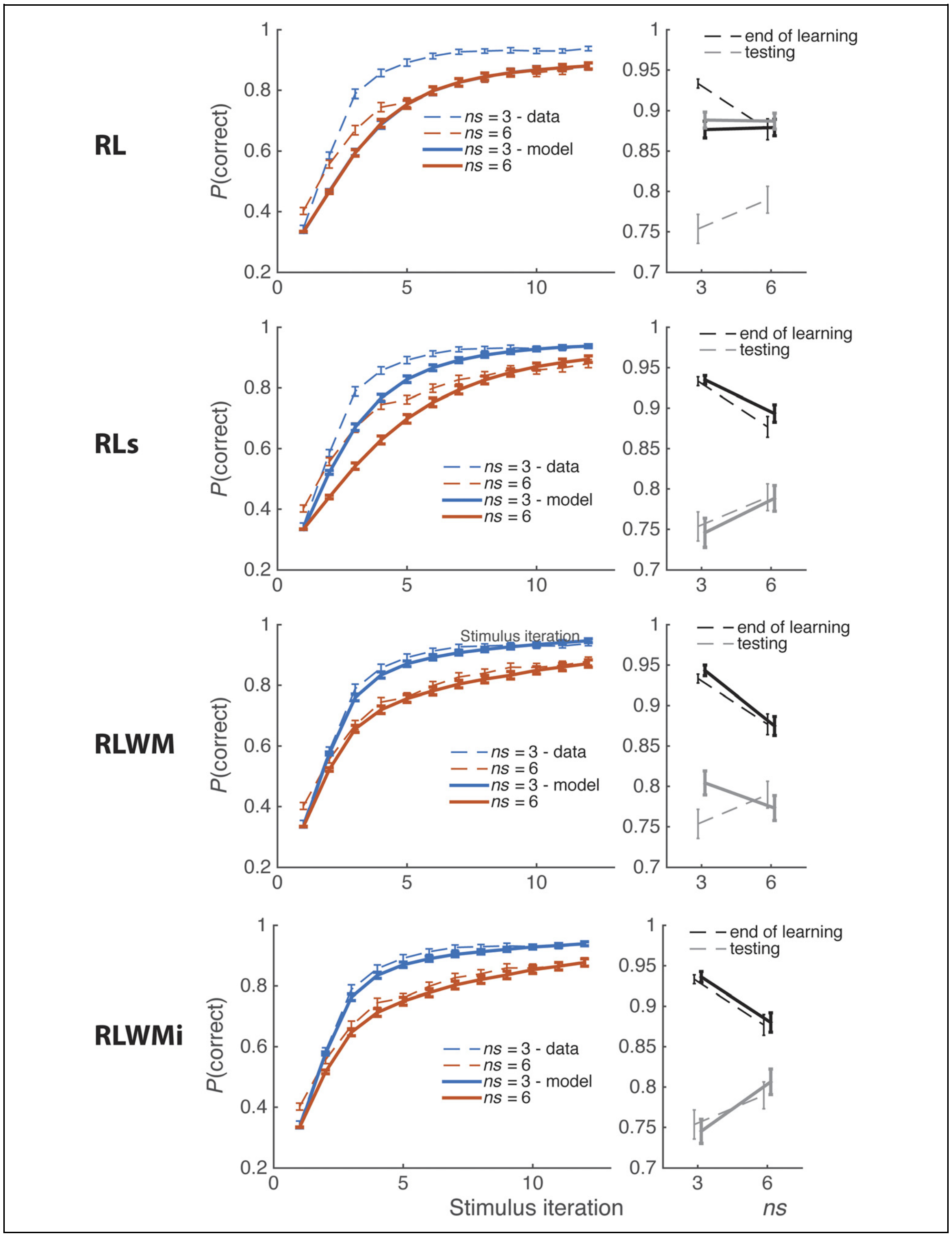


Figure 3. Model predictions. Model simulations with fit parameters. (Left) Proportion of correct trials as a function of stimulus iteration number, for set sizes *ns* = 3/6. (Right) Proportion of correct trials at asymptotic learning performance (last five iterations of a stimulus: black line) and during test phase (gray line). Simulations were run with best fit parameters, 100 times per participant. Models are RL (classic two-parameter RL), RLs (best model in the RL family, including two independent Q-tables for learning and testing and two learning rates per set size per learning process), RLWM (with independent WM and RL modules), and RWMi (with interacting modules). Dotted lines show participants' behavior; full lines, model simulations. Note that the simulated learning curves for the RL model overlap, showing no effect of set size.

RL + WM independent models. Models in the RLWM family include separate RL and WM modules and assume that learning phase choice is a mixture of the RL and WM policy, whereas testing phase choice follows RL policy.

The RL module of the RLWM models is a classic RL model as described above, characterized by parameters α and β, with the additional mechanisms of initial bias and perseveration.

The WM module stores information about weights between stimuli and actions, $W(s,a)$, which are initialized similarly to RL Q values. To model fast storage of information, we assume perfect retention of the previous trial's information, such that $W_{t+1}(s_t,a_t) = r_t$. To model delay-sensitive aspects of WM (where active maintenance is increasingly likely to fail with intervening time and other stimuli), we assume that WM weights decay at each trial according to $W_{t+1} \leftarrow W_t + \phi\,(W_0 - W_t)$. The WM policy uses the $W(s,a)$ weights in a softmax with added undirected noise, using the same noise parameters as the RL module.

Contrary to previous published versions of this model (Collins, Ciullo, et al., 2017; Collins et al., 2014; Collins & Frank, 2012), we cannot estimate WM capacity directly in this protocol, because we only sample set sizes 3 and 6. Thus, we model the limitations of WM involvement in choice with a fixed set-size-dependent mixture parameter η_{ns} for the overall choice policy:

$$P_{\text{learn}}(a|s) = \eta_{\text{ns}} P_{\text{WM}}(a|s) + (1 - \eta_{\text{ns}}) P_{\text{RL}}(a|s)$$

For the testing phase, we assume that $P_{\text{test}}(a|s) = P_{\text{RL}}(a|s)$.

The best model in this family thus includes eight parameters (softmax β, RL learning rate α, WM decay ϕ, *pers*, undirected noise ε, initial bias, two mixture parameters η_3 and η_6). This model predicts identical effects of set size in the learning and testing phases, with worse performance in lower set sizes (Figure 3, third row).

RL + WM interacting models. This family of models is identical to the previous one, with the exception that the WM module influences the RL computations. The RL module update is still assumed to follow $Q_{t+1}(s,a) = Q_t(s,a) + \alpha \times \delta_{t,}$. However, WM contributes cooperatively to the computation of the RPE δ_t by contributing to the expectation in proportion to WM's involvement in choice:

$$\delta_t = r_t - (\eta_{\mathrm{ns}} W_t(s,a) + (1 - \eta_{\mathrm{ns}})Q_t(s,a))$$

The best-fitting model in this family, RLWMi, has the same parameters as the no-interaction RL + WM models. This model predicts opposite effects of set size in the learning and test phases, with worse performance in lower set sizes (Figure 3, third row). We tested a variant (RLWMii) that assumes independent η_{ns} parameters for policy mixture and interaction mechanisms; it provided a significantly worse fit (Figure 4). We also explored a competitive interaction model, whereby WM inhibited RL computations by decreasing learning rate. This model fit equally well as RLWMi but cannot account for previous EEG findings (Collins & Frank, in press; see Discussion); thus, we only report here the cooperative interaction.

Model Fitting and Validation

We used the MATLAB constrained optimization function `fmincon` to fit parameters (the MathWorks Inc., Natick, MA). This was iterated with 20 randomly chosen starting points to increase the likelihood of finding a global rather than local optimum. All parameters were fit with constraints [0 1], except the softmax parameter β, which was constrained to [0 100].

We used the Akaike Information Criterion to penalize model complexity (Figure 4) (Akaike, 1974). Results were identical when using Bayesian Information Criterion (Schwarz, 1978), which was used to compute exceedance probability. Comparing the RL-only models, independent RLWM, interacting RLWMi, and double interacting RLWMii, the simple interacting RLWMi model was strongly favored with exceedance probability of 1-5e^{-6} over the whole group (Stephan, Penny, Daunizeau, Moran, & Friston, 2009).

Model selection alone is insufficient to assess whether the best-fitting model sufficiently captures the data. To test whether models capture the key features of the behavior (e.g., learning curves), we simulated each model with fit parameters for each participant, with 100 repetitions per participant then averaged to represent this participant's contribution (Figure 3).

RESULTS

Results from the learning phase replicated previous experiments (Collins & Frank, 2012; Figure 2A and D, top). Specifically, we found that participants learned to select correct actions in both set sizes (Figure 2A, top) but were slower to learn in blocks with a set size of ns = 6. This was characterized in a logistic regression analysis, which identified two main contributions to learning. First, RL was characterized by a positive sensitivity to reward history (number of previous correct trials; sign test, $p <$ 10e-4): The more previous correct choices they had, the more likely participants were to pick the correct choice on the current trial. Second, WM was characterized by a negative effect of set size and delay on performance since the last correct iteration of the current stimulus (both ps $<$ 10e-4): Participants were less likely to pick the correct actions under higher load or if there had been more intervening trials since they last chose correctly. Furthermore, we identified a practice effect, such that performance was higher in later blocks (sign test, p = .01). These results were also paralleled in RTs (Figure 2A, bottom), such that factors facilitating correct choice (reward history and

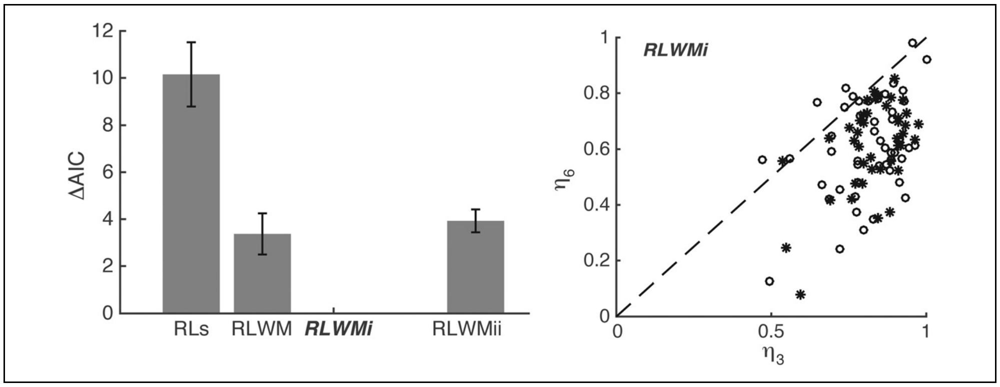


Figure 4. Model fitting. (Left) Difference in Akaike Information Criterion between different models and best model RLWMi. The RLs model is a flexible model including only RL mechanisms; the RLWM model includes an RL module and a WM module that are independent but compete for choice. RLWMi additionally includes an interaction, whereby WM contributes to RL computations. RLWMii allows separate weighting for WM's contribution to choice and RL computations. Error bars indicate *SEM*. (Right) Mixture weights η indicate contribution of WM to choice and RL computations in both set sizes for all participants (initial experiment: open circles; replication: stars). As expected under the hypothesis that the WM module represents WM, we observe consistently lower contribution of WM in high than low set sizes ($\eta_6 < \eta_3$).

block) also lead to faster choices ($p < 10\text{e-}4$ and $p = .002$, respectively) and factors making choice harder lead to slower choices (set size and delay; both ps $< 10\text{e-}4$). At its asymptote, performance was lower in high than low set sizes ($t(84) = 6.8$, $p < .0001$; 66/85 participants: $p < .0001$). This effect was coupled with higher RTs ($t(84) = 26.9$, $p < .0001$; 85/85 participants: $p < .0001$).

Model simulations showed that a classic RL model could not account for the learning phase effects (Figure 3, RL) and that, although more complex, single-process RL models can capture a qualitative effect of set size with set-size-dependent learning rates, they do not quantitatively capture the learning phase dynamics (Figure 3, RLs). In contrast, we replicate our previous finding that RLWM models can capture learning phase dynamics well (Figure 3, RLWM and RLWMi).

We next analyzed testing phase performance as a function of the set size in which an item had been learned. As expected from our hypothesis that learning relies on RL and WM, but testing on RL only, we found overall worse performance ($t(84) = 10.5$, $p < 10\text{e-}4$) in the testing phase compared with asymptotic performance in the learning phase as well as faster RTs ($t(84) = 21.1$, $p < 10\text{e-}4$). Furthermore, our theory assumes that learning in high-set-size blocks relies more on RL than in low-set-size blocks and that testing phase relies only on RL. Thus, we predicted that individual differences in testing phase behavior should be better predicted by individual differences in asymptotic learning phase performance in high than low set size blocks and that this should be true for stimuli learned in either set size. Unsurprisingly, a multiple regression analysis with both asymptotic set size 3 and 6 learning phase performance showed that set size 6, but not set size 3, was significantly predictive of set size 6 test performance ($t(84) = 5.06$, $p < 10\text{e-}4$ for $ns = 6$; $t(84) = 1.8$, $p > .05$ for $ns = 3$). Surprisingly, but confirming our prediction, we also found that set size 3 testing phase performance was predicted by set size 6, but not set size 3 asymptotic learning phase performance ($t(84) = 4.5$, $p = .0000$ for $ns = 6$; $t(84) = -0.02$; $p = .98$ for $ns = 3$). These results support our hypothesis that testing phase performance relies on RL, which is more expressed during learning of set size 6 than 3.

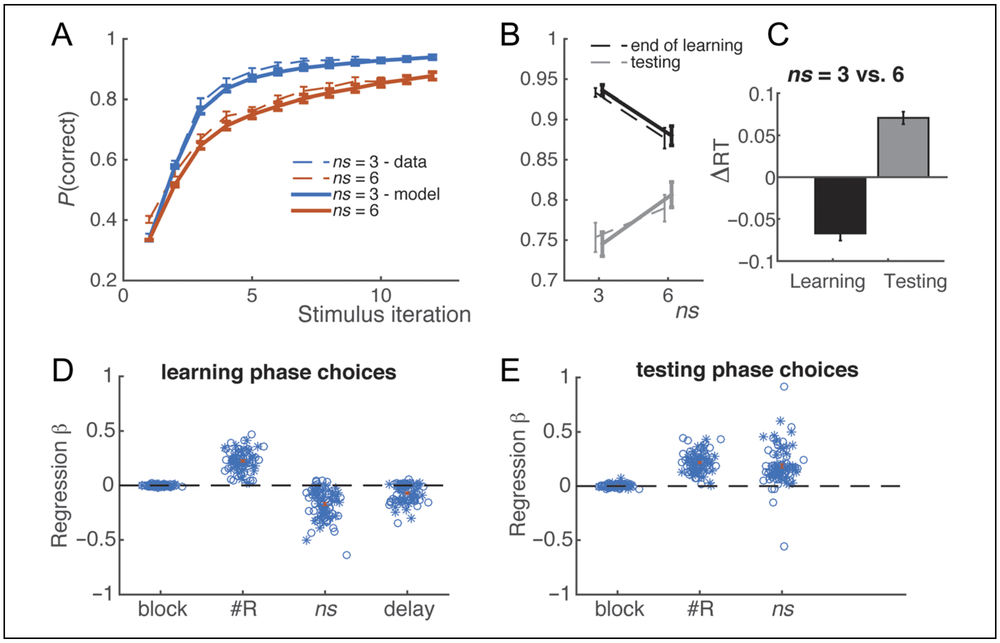
Next, we investigated testing phase performance as a function of set size of the block during which the stimulus was learned. It is important to remember that, if testing phase performance reflected the history of choices and rewards during learning, participants should be better able to select correct actions for stimuli in low set sizes rather than in high set sizes (after their asymptotic learning performance). Instead, we found that participants were significantly better at selecting the appropriate action for items they learned in high set sizes (Figure 2B; $t(84) = 3.8$, $p = .0003$; 58/85 participants: sign test, $p = .001$), indicating a counterintuitive robustness of learning under high load. This was also visible in RTs, which were faster for items learned under high load (Figure 2B; $t(84) = 3.5$, $p = .0008$; 57/85 participants: $p = .002$).

We confirmed these results with multiple regression analyses, using learning block, learning set size, and asymptotic average rewards as predictors. Results showed that learning block and reward history accounted for a significant variance in testing phase performance and RTs (Figure 2D; sign tests, ps $< 10\text{e-}4$), with effects in the same direction as learning phase performance and RTs, reflecting variance in the learning process. However, set size predicted variance in the testing phase in the opposite direction from the learning phase (Figure 2D; better choices, $p < 10\text{e-}4$; faster RTs, $p = 2.10\text{e-}4$). Together, these results confirm our prediction that, despite apparent successful learning in low set sizes, stimulus–action associations were formed in a way that was stronger in high set sizes, as observed in testing phase performance.

Next, we sought to confirm that these effects were not due to differences in reward history. First, we limited testing phase analysis to items where the participant chose correctly for all last six iterations (thus reaching 100% asymptotic performance in both set sizes). Within this subset, we again observed better test performance in high-set-size stimuli, with a stronger effect ($p < 10\text{-}4$, $t(84) = 7.6$). Second, we asked whether higher performance in set size 6 might be accounted for by participants better avoiding choices that were unrewarded during learning, which would have been experienced more in set size 6 than in set size 3. However, we found that the types of errors made by participants in both set sizes were not different ($t(84) = 0.01$, $p = .99$) and significantly suboptimal (one-sample t test vs. chance: both ts > 12, proportion of optimal error trials = 27%; see Methods). Thus, superior performance in high set sizes was not due to a better avoidance of incorrect actions due to higher sampling of errors during learning. Indeed, RLWM models with no interaction between RL and WM predicted the opposite effect of set size in the testing phase (Figure 3, RLWM).

Instead, we hypothesized that the reversal in the effect of set size on performance between learning and testing was indicative of WM interfering with RL computations during learning. Specifically, we hypothesized that, in low-set-size blocks, which were putatively within WM capacity, the ability to solve the learning problem with WM would lead to interference with RL computations. We propose a mechanism whereby WM is able not only to store stimulus–action associations but also to predict a correct outcome when this association is used. This prediction is used cooperatively in a mixture with the RL expectation to compute RPE (Figure 1C), and thus when WM is ahead of RL, it decreases positive RPEs and effectively impedes learning in the RL process (Collins & Frank, in press). This would then lead to less well-learned associations in low compared with high set sizes. We characterized the contributions of WM and RL to choice and to the RPE with a single mixture parameter for

Figure 5. RLWMi validation. Model simulations with fit parameters. (A) Model simulations reproduce learning curves. (B and C) Model simulations reproduce the opposite effects of set size *ns* between the learning and testing phases, for both choices and RTs. (D and E) Logistic regression analysis of the learning and testing phase choices captures behavioral effects (Figure 2), including the opposite effects of set size on performance.



each set size, η_{ns} (see Methods for full model description). If this mixture parameter represents contributions of capacity-limited WM, we should observe $\eta_6 < \eta_3$. This is indeed what we observed with parameters fit on individual participants' choices (Figure 4, right).

We tested this model (RLWMi) against three other main models (as described in the Methods section). The first alternative (RLs) assumed only RL processes and was made flexible enough to be able to reproduce all qualitative effects observed empirically. This required assuming that two independent sets of association weights were learned in parallel, one used during learning and the other used during testing, and that learning rates were different for both as well as for different set sizes. The second alternative model (RLWM) was similar to the main model (RLWMi), but without the interaction for learning. The last alternative model (RLWMii) was identical to RLWMi but offered flexibility in separately parameterizing the contribution of WM to choice and learning. We fitted participants' behavior with the three models and found that RLWMi fit significantly better than the other three models (exceedance probability = 1). Model simulations (Figure 3) confirmed that RLWMi provided the best qualitative and quantitative accounts of the data. These results confirm that WM is needed to account for learning behavior and that an interference with RL is the best way to account for counterintuitive testing phase effects. It is important to note that letting the contributions of WM to choice and to RL be independent does not capture additional variance in behavior, hinting that these two functions might share a single, coupled mechanism.

To validate the RLWMi model, we simulated it with individual participants' fit parameters (100 times per participant). Simulations provided a good qualitative and quantitative fit to the choice results in both the learning and testing phases. Specifically, the simulations produced learning curves that were very close to participants' (Figure 5A) and reproduced the opposite set size effects in the asymptotic learning phase and the testing phase (Figure 5B, D, and E). We did not capture the practice effect (block; Figure 5D and E). We also simulated RTs by assuming a negative linear dependence on the model-determined probability of the choice, such that faster RTs occurred for choices with higher confidence. Using these simulated RTs, we reproduced the observed pattern whereby RTs are faster for low set sizes than high set sizes during learning, but the opposite is true for the testing phase (Figure 5C). This is because, during learning, the WM contribution to choice leads to more confidence in the choices and faster RTs, but the higher WM interference during learning leads to less well-learned *Q* values for low set sizes, which translates to slower RTs during testing. It is important to note that the model was fit only to the choices, not RTs, so this is an independent test of the model's ability to capture empirical data.

DISCUSSION

Our new experimental protocol allows us to demonstrate a surprising finding: Associations learned in a more complex problem end up being learned more robustly and are better retained in the long term, than easy-to-learn associations. This finding provides behavioral evidence for an interaction between WM and RL. Specifically, we showed previously that RL and WM compete for choice during learning (Collins et al., 2014; Collins & Frank, 2012). Here, we show an additional interaction between them whereby WM impedes RL computations. These new results behaviorally and computationally support our previous observations that WM and RL are not independent

This is shown in the test phase. How do we know this is BG/RL learning?

I don't understand why!

modules but that RL neural signals are weakened by WM use (Collins & Frank, in press; Collins, Albrecht, et al., 2017; Collins, Ciullo, et al., 2017). It also strengthens our previous result showing that stimulus value was better learned in high set sizes (Collins, Albrecht, et al., 2017) but offers a more robust computational account for this finding.

It may be that AG is the opposite of WPT: not rapid WM learning

What happens after WM - where does information go? What do they mean by WM learns?

Similar story as in Keramati et al

How is this interpreted for complex skills?

WM and RL implement different trade-offs for learning: WM allows for very fast learning of information that is not durably retained, whereas RL allows for slow, integrative learning of associations that are robustly stored. Previous models assumed that humans can benefit from the best of both worlds by shifting the weight given to each system as a function of their reliability (Collins, Ciullo, et al., 2017; Collins et al., 2014; Collins & Frank, 2012). Specifically, assuming that the effortless RL process simply occurs independently in the background, we can use WM to the maximum of its reliability for learning and use RL first as a backup but, as it becomes more reliable than WM, shift to "automatized" RL behavior only. The results presented here show instead that the trade-off cannot be completely eliminated by carefully arbitrating between RL and WM during learning: The use of WM in easy problems weakens RL learning and thus leads to faster learning at the cost of long-term retention.

We proposed a computational mechanism by which WM may impede RL learning. Despite its negative effect on long-term learning, this mechanism can be thought of as cooperative. Indeed, we suggest that, when an association is held in WM, WM can also contribute to corresponding reward expectations. Our computational mechanism assumes that WM's expectation is weighted with RL's expected value and that this mixture expectation is then used to compute RL's RPE. Thus, when WM is reliable and learns faster than RL, this mechanism generates lower RPEs in correct trials than an independent RL mechanism would, which in turn leads to a weaker update of associations in the RL system. This mechanism is compatible with our observations in an EEG experiment, where trial-by-trial neural markers of WM use predicted lower markers of RPEs (Collins & Frank, in press).

We showed that this cooperative interaction accounted for trial-by-trial choices during learning and testing better than models assuming no interactions. However, other interaction mechanisms could also be considered—in particular, a competitive mechanism provides a similar fit to participants' choices (Collins & Frank, in press). This mechanism simply assumes that the RL learning rate is decreased, in proportion to WM contributions to choice. This leads to slower RL learning, not due to weakened RPEs as in the cooperative mechanism but due to a weaker effect of reward prediction learning on updates. Competition and cooperation mechanisms make separable predictions for neural signals: The competition mechanism predicts that RPEs will decrease slower in low set sizes because of the slow learning rate, whereas the cooperation mechanism predicts that they will decrease faster in low set sizes because of accurate WM predictions. EEG results confirmed the latter prediction (Collins & Frank, in press), thus supporting the cooperation mechanism prediction. However, it will be important in future work to show behavioral evidence disambiguating the two mechanisms.

This leaves open an important question: Are there situations in which a cooperative mechanism might be beneficial? In our experimental protocol, it seems suboptimal, as it leads to weakened learning in the long term. RL algorithms are only guaranteed to converge to true estimates of expected value if the RPE is not tampered with; interference may bias or slow computations, as is seen here. It is thus puzzling that we might have evolved an interaction mechanism that actively weakens one of our most robust learning systems. Future research will need to determine whether this bias might be normative in more natural environments—for example, it is possible that situations in which learning is required to be very fast are also volatile environments, where we might need to change our behavior quickly. In that case, not having built as strong an association might allow for a more flexible behavior. Another hypothesis is that this interaction reflects constraints of neural network implementations and is thus a side effect of another normative mechanism: specifically, that the contribution of WM to choice, which helps learn faster in low set sizes, is not separable from its contributions to the reward expectation (Figure 1C). Although we do not have direct evidence for this hypothesis, our model fitting results provide a clue in its favor: A more flexible model that allowed contributions of WM to choice and RL to be uncoupled did not provide a better fit, and the additional degrees of freedom led to overfitting. Thus, no additional variance was captured by letting choice and learning interactions be separable, pointing to the possibility that they are indeed coupled mechanisms. Future research will need to clarify this.

We focused on how two neurocognitive systems, WM and RL, worked together for learning, highlighting the effects of their interactions in a testing phase where only RL was used. However, it is likely that one other system—long-term memory—contributes to testing performance and potentially also to learning (Bornstein et al., 2017; Bornstein & Norman, 2017). Indeed, others have shown that long-term memory encoding may compete for resources with RL processes (Wimmer, Braun, Daw, & Shohamy, 2014; Poldrack & Packard, 2003), and other interactions may be possible (for a review, see Gershman & Daw, 2017). Here, we observed in the testing phase that participants performed better for associations learned closer to the testing phase, an effect reminiscent of the well-documented recency effect in long-term memory recall (Sederberg, Howard, & Kahana, 2008). Our model currently does not capture this effect or other potential contributions of long-term memory. Although including it is beyond the scope of this work, it will be important in future research to investigate how this third mechanism interacts with RL and WM for learning.

In summary, our results show a counterintuitive but robust (and replicable) finding—that, although learning under high load is slower and more effortful, it actually allows for better long-term learning and retention. This appears to be due to the fact that faster learning under low load cuts the corner with WM and, by doing so, undermines more robust encoding of associations via RL. Our findings highlight complex interactions between multiple learning systems not only at the level of decisions but also at the level of learning computations. When learners arbitrate in favor of fast and efficient WM use over RL in simple situations, they simultaneously undermine the computations from this slower but more robust system, leading to worse long-term performance. This result may have an important implication in numerous domains, as learning is an important part of our daily lives—for example, in educational settings. Understanding how multiple systems work together for learning is also a crucial step in identifying the causes of learning dysfunction in many clinical populations and thus better targeting treatments.

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